



Sternal pore plates (glandular areas) of male Thripidae (Thysanoptera)

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Abstract

Variation is illustrated in the specialized areas known as pore plates (glandular areas or *areae porosae*) that occur on the sternites of males of many Thysanoptera species, and the occurrence of these structures in genera of Thripidae is tabulated. Pore plates are present in more than 60% of genera in this family, and known to be absent in about 20%; males are not known in a further 20% of the genera. In families of Terebrantia other than Thripidae, pore plates also occur in Fauriellidae, Heterothripidae and Adiheterothripidae, but not in Aeolothripidae, Melanthripidae and Uzelothripidae. Females in a very few species of Thripidae have pore plates apparently similar to those of males.

Key words: glandular areas, *areae porosae*, pore plates, Thripidae

Introduction

The males of many species of Thysanoptera have, on one or more abdominal sternites, porose structures that have been referred to as “glandular areas” or “*areae porosae*”. The more precise and descriptive term “pore plate” was used for these structures (Heming, 1970) in a brief account of their cellular structure in the thripid *Frankliniella fusca*. This term was also adopted more recently (El-Ghariani & Kirk, 2008) in morphological studies on another thripid, *Frankliniella occidentalis*, as well as in a taxonomic revision of a large group of Thripidae (Mound & Masumoto, 2009). Pore plates seem to be associated with subcuticular glandular cells that are probably the source of aggregation pheromones secreted by males (Kirk & Hamilton, 2004; Hamilton et al., 2005), and such pheromones are presumably important in sexual behaviour (Milne et al., 2002; Webster et al., 2006). Moreover, pheromones seem likely to hold considerable potential for pest control and pest monitoring through the manipulation of sexual behaviour (Hamilton & Kirk, 2003). Such techniques, based on disruption of chemical communication, hold the prospect of obviating problems associated with insecticide resistance. The limited purpose of this article is to record the distribution of pore plates in males of genera throughout the Thripidae, the family that includes most Thysanoptera pest species, with a view to facilitating future studies on evolutionary patterns in behaviour and body structure.

The pore plates considered here are particularly those found in members of the suborder Terebrantia of the Thysanoptera. In the Tubulifera, the other suborder of Thysanoptera, males of many species in the subfamily Phlaeothripinae have a porous area (Figs 1, 2) occupying much of the eighth sternite (Mound & Walker 1986; Cavallieri & Kaminski, 2007), and some species of Tubulifera have on various sternites reticulate markings that are possibly associated with glandular cells (Okajima, 1981; Mound & Palmer, 1983). In contrast, pore plates among the Terebrantia are usually discrete areas situated medially on one or several sternites. Their superficial appearance often provides character states for species-level taxonomic discrimination (Wilson, 1975; zur Strassen, 2003), but the distribution of pore plates among genera has never been documented. Moreover, details of the internal structure of pore plates have been investigated in very few species (Klocke, 1926; Bode, 1978; Sudo & Tsutsumi, 2002, 2003; Shitani & Tsutsumi, 2005, 2006; El-Ghariani & Kirk, 2008), and thus questions remain concerning the homology between the wide range of forms illustrated here

(Tables 1, 2; Figs 4–39). For example and even with the Thripidae, Shitani & Tsutsumi (2005) indicate differences in the internal structure of pore plates between *Tenothrips frici* and three species in the genera *Thrips* and *Frankliniella*, and suggest that this might involve different secretory mechanisms.

In order to facilitate this discussion, authority names for all taxa are omitted; full nomenclatural details for these taxa are readily available from the Catalogue of World Thysanoptera on the web (Mound, 2009).

Pore plates among the Terebrantiate families

Within the insect order Thysanoptera, members of three families retain the largest number of character states in a plesiomorphic condition: the Merothripidae, Melanthripidae and Aeolothripidae (Mound & Morris, 2007). Males of species in these families all lack sternal pore plates, as do males in the only known species of the enigmatic family Uzelothripidae. Presence of these structures is thus possibly the derived condition within Thysanoptera. However, males remain unknown for most Merothripidae, and the only known males of species in this family have on the dorsal surface of the head an extensive area (Fig. 3) that appears to have a similar porous structure to that of the sternal pore plates of Thripidae (Moritz, 1984). Males in the two families Melanthripidae and Aeolothripidae have the first abdominal segment much longer than wide, in contrast to males in the other families. This structural difference is possibly associated with differences in mating position and sexual behaviour.

Of the remaining four terebrantiate families of Thysanoptera, the only species of Fauriellidae for which a male is known, and all of those species of Heterothripidae and Adiheterothripidae for which males are known (Figs 4–5), have pore plates on one or more abdominal sternites. Pore plates of males in these three families are situated anterior to the sternal antecostal ridge (Mound et al., 1980), whereas in the large and diverse family Thripidae the pore plates are generally on the discal area of the sternites (Figs 35–38). Homology between these two conditions remains unclear, and this study is focused on the variation found among members of the Thripidae. In this family, although pore plates are generally found medially on the sternites of males, there is considerable variation between taxa, both in the precise position as well as in the form and numbers of the structures involved. This variation is discussed separately for each of the four recognized thripid subfamilies (Mound, 2009): Panchaetothripinae, Dendrothripinae, Sericothripinae and Thripinae.

Pore plates among Dendrothripinae and Sericothripinae

The subfamily Dendrothripinae comprises about 100 species in 10 genera, and these species all appear to breed on leaves not in flowers. Males are known for species in only six of the genera (*Dendrothrips*, *Edissa*, *Ensiferothrips*, *Filicopsotrips*, *Leucothrips*, *Pseudodendrothrips*), and these males all lack sternal pore plates (Mound, 1999). The Sericothripinae comprises about 140 species in three genera, although this generic classification is not considered satisfactory (Mound & Tree, 2009). Well-developed, transversely oval pore plates, apparently similar in structure to those found in the Thripinae, are present in a few species. However, the number of sternites involved is not constant between species, and each small circular pore plate on sternites IV–VII in *Sericothrips staphylinus* (Fig. 6) is sometimes sub-divided into two.

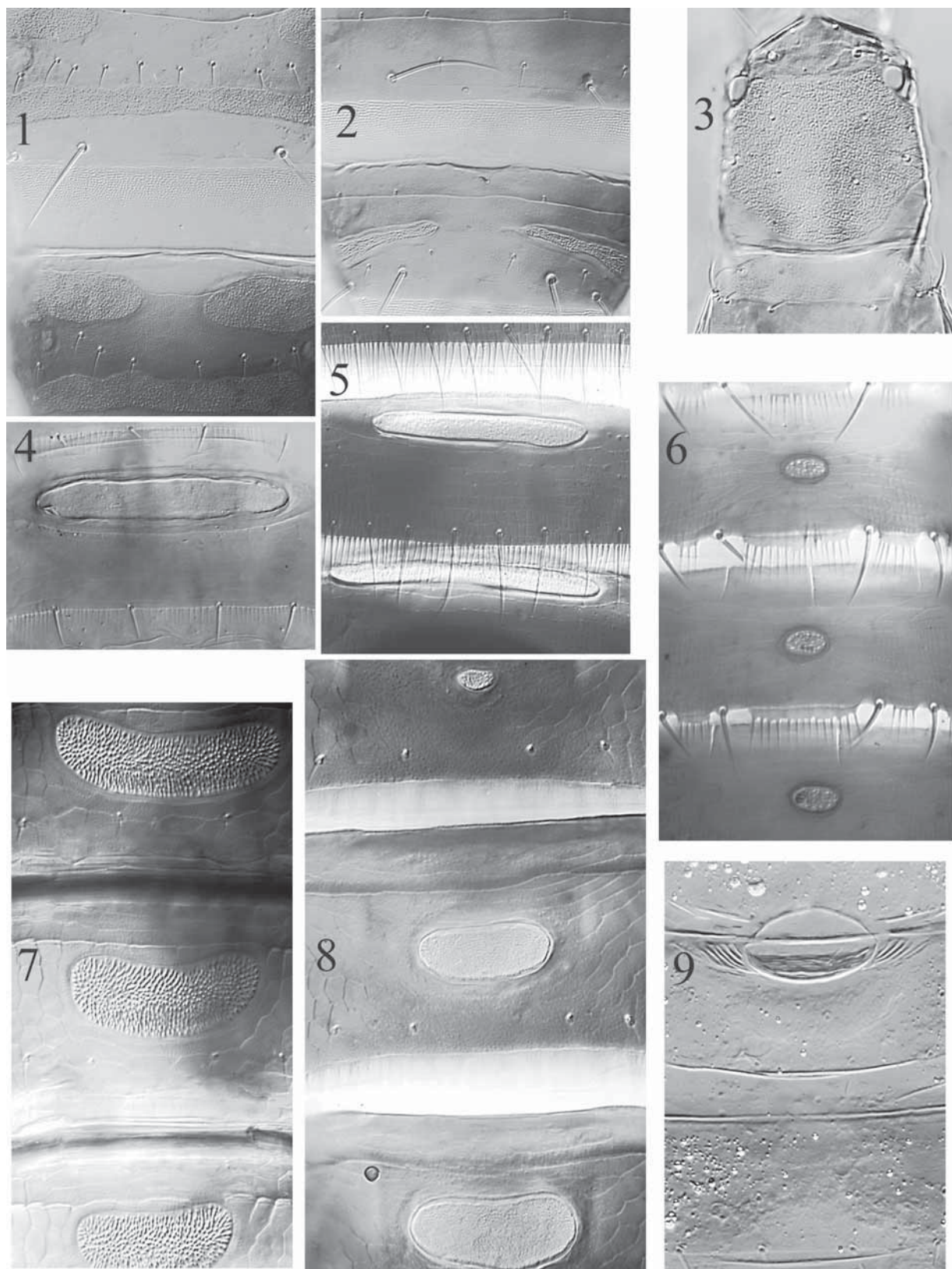
Pore plates among Panchaetothripinae

The Panchaetothripinae, comprising about 130 species in 36 genera, is the subfamily that includes the Greenhouse Thrips and several other leaf-feeding pest species. Males are not known for eleven of the genera (Table 1), but the presence, absence and form of pore plates in this small group are remarkably variable, both within and between genera (Wilson, 1975). Pore plates are lacking in males of five genera that include a total

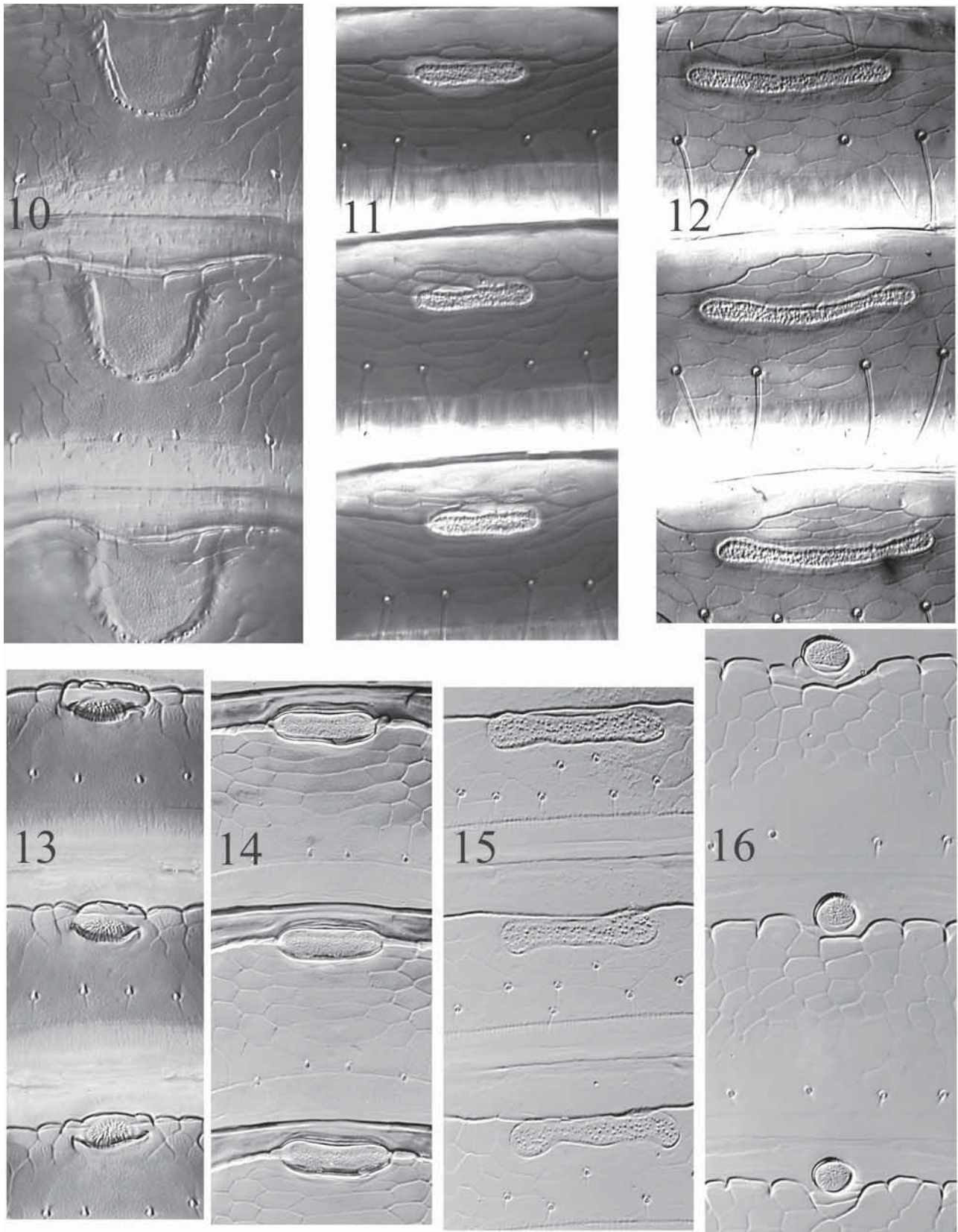
TABLE 1. Pore plate distribution in males of Thripidae-Panchaetothripinae genera.

1. Pore plate medially on some sternites;
2. Pore plate on antecostal ridge;
3. Pore plates lacking;
4. Male not known or information not available.

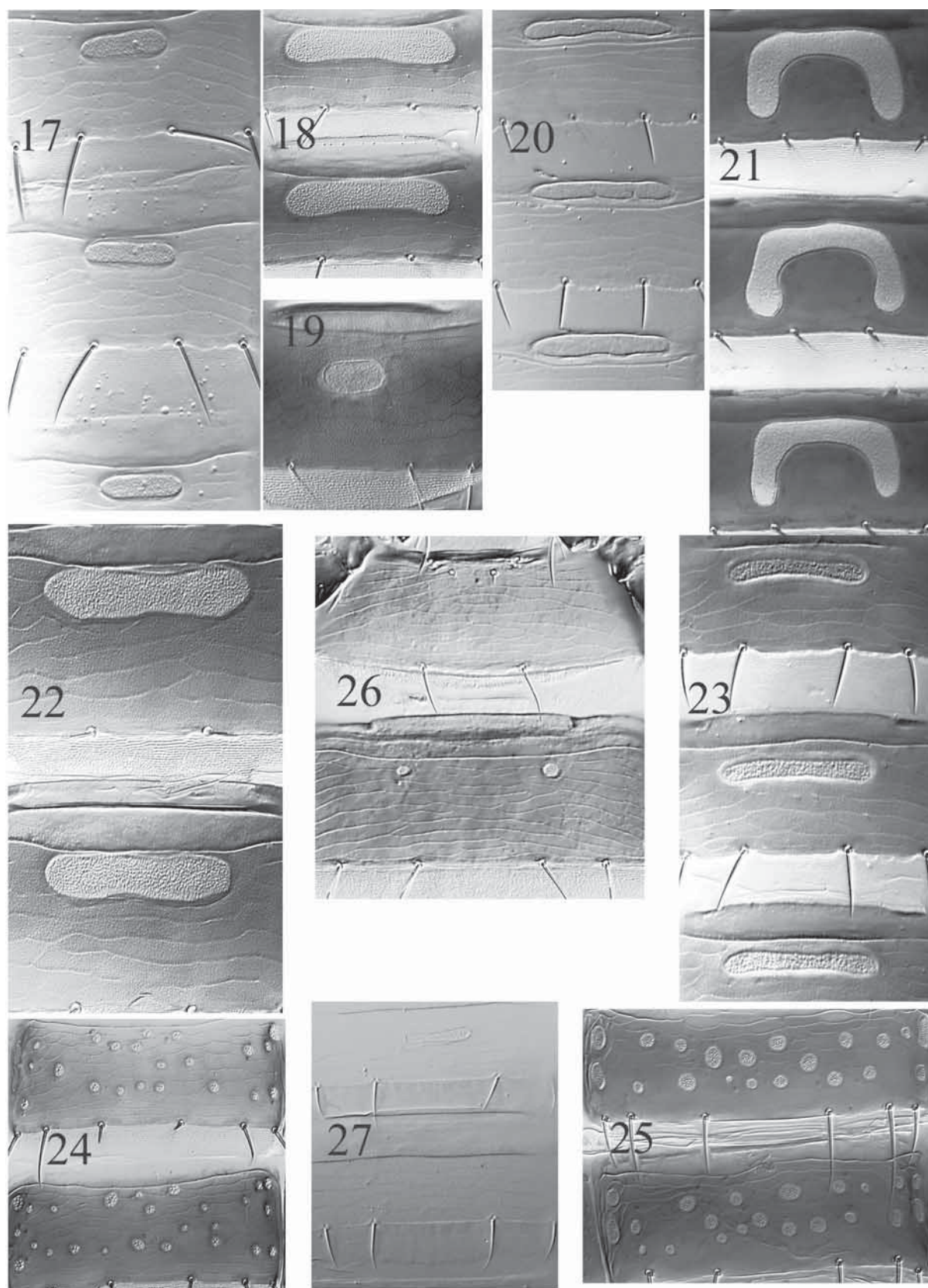
| | 1 | 2 | 3 | 4 |
|-------------------------|----|---|---|----|
| <i>Anisopilothrips</i> | | | | + |
| <i>Aoratothrips</i> | | | | + |
| <i>Arachisothrips</i> | + | | | |
| <i>Astrothrips</i> | + | | + | |
| <i>Australothrips</i> | | | + | |
| <i>Bhattithrips</i> | | + | + | |
| <i>Brachyurothrips</i> | + | | | |
| <i>Caliothrips</i> | + | | | |
| <i>Chaeturothrips</i> | | | | + |
| <i>Copidothrips</i> | | | | + |
| <i>Dinurothrips</i> | + | | | |
| <i>Elixothrips</i> | | | | + |
| <i>Euhydrothrips</i> | + | | | |
| <i>Euidothrips</i> | | | | + |
| <i>Galeothrips</i> | | | + | |
| <i>Helionothrips</i> | + | | + | |
| <i>Heliothrips</i> | + | | | |
| <i>Hemingia</i> | + | | | |
| <i>Hercinothrips</i> | + | | + | |
| <i>Hoodothrips</i> | | | + | |
| <i>Monilothrips</i> | | | + | |
| <i>Moundothrips</i> | | + | | |
| <i>Noathrips</i> | + | | | |
| <i>Oneilliella</i> | | | | + |
| <i>Opimothrips</i> | | | | + |
| <i>Panchaetothrips</i> | + | | | |
| <i>Parthenothrips</i> | + | | | |
| <i>Phibalothrips</i> | | + | | |
| <i>Retithrips</i> | + | | | |
| <i>Rhipiphorothrips</i> | | + | | |
| <i>Selenothrips</i> | + | | | |
| <i>Sigmothrips</i> | | | | + |
| <i>Stannardiola</i> | | | | + |
| <i>Tryphactothrips</i> | | | | + |
| <i>Xestothrips</i> | + | | | |
| <i>Zaniothrips</i> | | | + | |
| Totals | 16 | 4 | 9 | 11 |



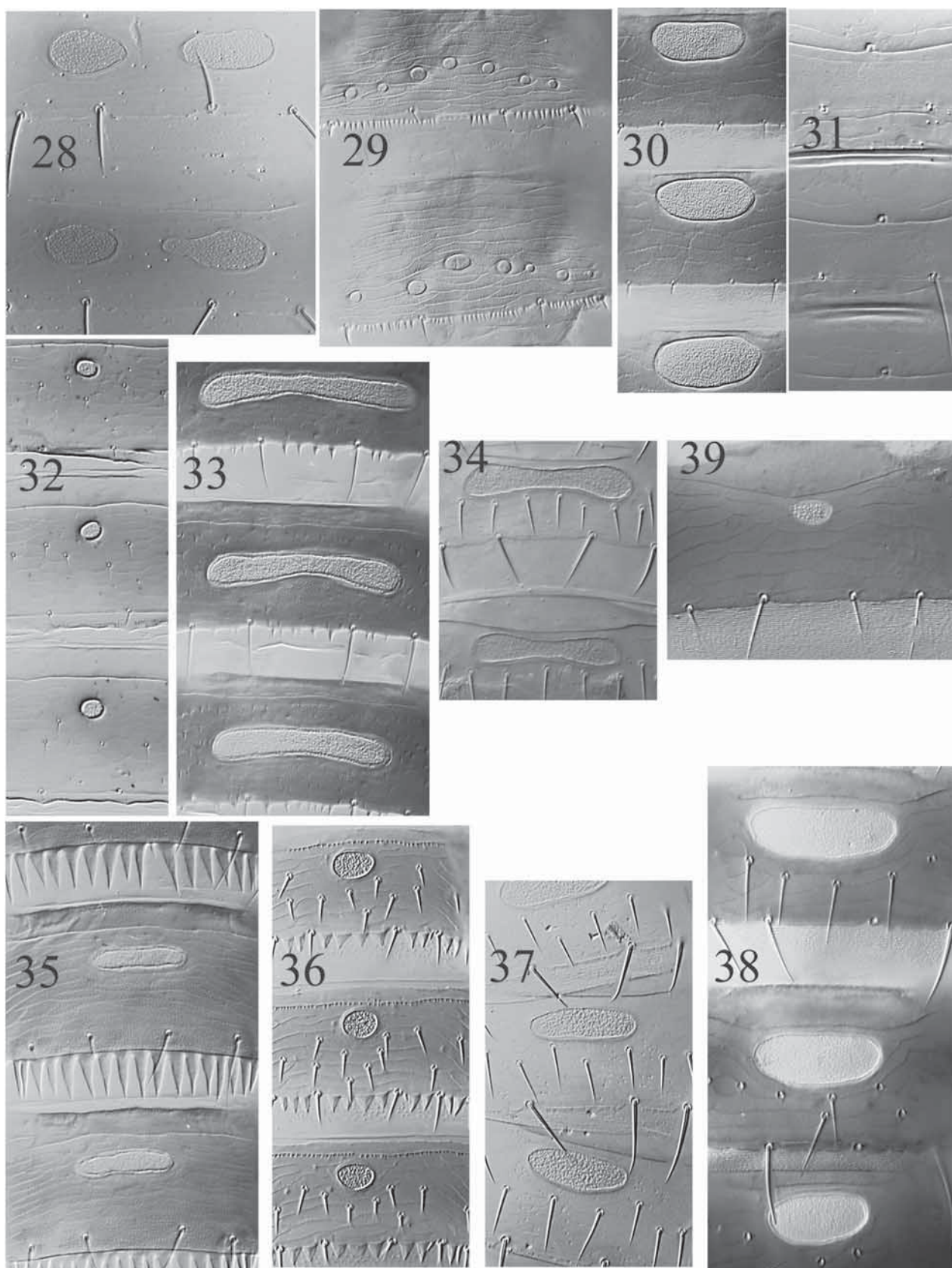
FIGURES 1–9. Pore plates of male Thysanoptera. Sternites VII–VIII: (1) *Holopothrips tabebuia* (Phlaeothripidae). (2) *Psalidothrips taylori* (Phlaeothripidae). (3) head, *Merothrips floridensis* (Merothripidae). (4) Sternite VII *Holarthrothrips josephi* (Adiheterothripidae). (5) Sternites VII–VIII *Heterothrips peixotoae* (Heterothripidae). (6) Sternites IV–VI *Sericothrips staphylinus* (Sericothripinae). Panchaethripinae sternites IV–VI, 7–8: (7) *Heliothrips haemorrhoidalis*; (8) *Parthenothrips dracaenae*. (9) Sternites III–IV *Desertathrips chuquiraga* (Thripinae).



FIGURES 10–16. Sternal pore plates of male Panchaetothripinae. (10) *Astrothrips stannardi*. (11) *Caliothrips fasciatus*. (12) *Caliothrips phaseoli*. (13) *Moundothrips apterygus*. (14) *Phibalothrips longiceps*. (15) *Prosopothrips chilensis*. (16) *Rhipiphorothrips cruentatus*.



FIGURES 17–27. Sternal pore plates of male Thripinae 17–25: (17) *Frankliniella occidentalis*. (18) *Frankliniella insularis*. (19) *Taeniothrips orionis*. (20) *Lomatothrips pinopsidis*. (21) *Parabaliotrips newmani*. (22) *Kakothrips pisivorus*. (23) *Pseudanaphothrips achaetus*. (24) *Pezothrips kellyanus*. (25) *Yoshinothrips pasekamui*. Pore plates on sternite III of female Thripinae 26–27: (26) *Frankliniella australis*. (27) *Chaetanaphothrips signipennis*.



FIGURES 28–39. Sternal pore plates of male Thripinae 28–38: (28) *Dichromothrips smithi*. (29) *Organothrips indicus*. (30) *Organothrips wrighti*. (31) *Tusothrips sumatrensis*. (32) *Limothrips cerealium*. (33) *Stenchaetothrips biformis*. (34) *Thrips hawaiiensis*. (35) *Fulmekiola serrata*. (36) *Microcephalothrips abdominalis*. (37) *Thrips australis*. (38) *Thrips atratus*. (39) Sternite III of female *Thrips knoxi*.

of eight species, *Australothrips*, *Galeothrips*, *Hoodothrips*, *Monilothrips* and *Zaniothrips*. In *Helionothrips*, they are absent in some species, but in others are circular on sternites VI–VIII, or VII–VIII, or only on VIII. Similarly variable are the species of *Hercinothrips*, with pore plates absent in some species, transverse in others but reduced to a small circle in a few (Wilson, 1975). In *Bhattithrips*, with three described and two known but undescribed species, pore plates are absent in one species but present on the antecostal ridge in two species; males are not known for the other two species. Pore plates occur on the sternal antecostal ridges also in males of *Moundothrips*, *Phibalothrips* and *Rhipiphorothrips* (Figs 13, 14, 16), but they are almost circular, and in *Moundothrips apterygus* they appear to be recessed into an invagination. These structures are transverse to broadly oval in the males of *Arachisothrips*, *Brachyurothrips*, *Heliothrips* (Fig. 7), *Panchaetothrips*, *Parthenothrips* (Fig. 8), *Retithrips* and *Selenothrips*. They are also transverse in some species of *Caliothrips* (Figs 11, 12), but are circular in a few members of that genus (Wilson, 1975). *Hemingia*, although apparently related to *Astrothrips*, is described as having a pair of uniquely longitudinal linear areas on sternites VI–VIII of males. In *Dinuurothrips*, *Noathrips* and most *Astrothrips* males have larger pore plates, although the photomicrograph given here (Fig. 10) suggests that description of these as “arcuate” (Wilson, 1975) may be a misinterpretation of the thickened margins of the plates. Currently, there seem limited systematic patterns in the presence and form of male pore plates in this subfamily.

Pore plates among Thripinae

The Thripinae, with 230 genera and 1600 species, is by far the largest of the four subfamilies of Thripidae. The species have a wide range of biologies, but are mainly either flower- or leaf-feeding, with a few species either obligate or facultative predators on other small arthropods. The distribution of male pore plates among the genera of this subfamily is indicated in Table 2.

One large group of species in which males lack pore plates is the *Scirtothrips* genus-group, recognized by Masumoto & Okajima (2007) as comprising ten genera (*Anascirtothrips*, *Biltothrips*, *Cercyothrips*, *Drepanothrips*, *Ephedrothrips*, *Parascirtothrips*, *Scirtidothrips*, *Scirtothrips*, *Sericopsorthrips*, *Siamothrips*). Species in these genera are leaf-feeding, a habit shared with the Dendrothripinae mentioned above that also lack pore plates. Males of species in the group of genera *Exothrips*, *Parexothrips* and *Rhamphothrips* also lack pore plates, and these species also seem to be associated with young leaf buds. However, the shared absence of pore plates in these unrelated groups seems unlikely to be directly associated with their shared habits. Males also lack pore plates in the Old World genus-group of thrips that breed in the flowers of Fabaceae (*Megalurothrips*, *Odontothrips* and *Odontothripiella*). Most of the other genera listed in Table 2 as lacking male pore plates cannot easily be arranged into related groups of more than two or three genera. Thus *Craspedothrips* and *Filipinothrips* are closely related (Tyagi et al., 2008), as are *Bregmatothrips* and *Sorghothrips*.

More interestingly, there are several genera in which males of some species have pore plates, yet males of other species lack these structures, such as *Eremiothrips*, *Limothrips*, and *Parabaliouthrips*. In one species in the latter genus, *P. newmani*, the males have large sternal pore plates (Fig. 21), and commonly these males have been seen forming “leks” on leaf buds to which females are attracted for mating (Gillespie et al., 2002). In contrast, males of a flower-living species in this genus, *P. setifer*, have no pore plates and do not form aggregations. Presence or absence of pore plates has even been noted between populations of *Brooksithrips chamaedoreae* that are considered to be conspecific (Retana-Salazar & Mound, 2005).

The Asian *Trichromothrips* genus-group was defined by Masumoto & Okajima (2005) primarily on female character states (*Cricothrips*, *Neocorynothrips*, *Octothrips*, *Okajimaella*, *Paithrips*, *Simulothrips*, *Trachynotothrips*, *Trichromothrips*, *Watanabeothrips*, and *Yoshinothrips*). The males of species in these genera all have multiple small pore plates (Fig. 25) on the sternites (Table 2 Column 7). To these 10 genera were also added *Laplothrips* and *Takethrips*, in which males are not known, and *Pteridothrips* in which males have only three small round pore plates. In contrast to this clear lineage, several apparently unrelated thrips

TABLE 2. Pore plate distribution in males of Thripidae-Thripinae genera.

1. Pore plate medially on sternites III + IV + V (\pm VI, VII & VIII);
2. Pore plate medially only on sternites indicated;
3. C-shaped pore plate on sternites III + IV + V (\pm VI & VII);
4. Two or three pore plates on several sternites;
5. Multiple small pore plates on at least III-VI;
6. Pore plate on antecostal ridge of at least IV-VI (rarely only II);
7. Gland aperture on antecostal ridge of III (no pore plate);
8. Neither pore plates nor glandular structures;
9. Male not known or information not available.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|-------------------------|---|-----|---|---|---|---|---|---|---|
| <i>Abacothrips</i> | | | | | | | | | + |
| <i>Acremonothrips</i> | | | | | | | | + | |
| <i>Adelphithrips</i> | + | | | | | | | | |
| <i>Afrothripiella</i> | | | | | | | | | + |
| <i>Agalmothrips</i> | + | | | | | | | | |
| <i>Agerothrips</i> | | | | | | | | + | |
| <i>Agriothrips</i> | | | | | | | | | + |
| <i>Agrostothrips</i> | + | | | | | | | | |
| <i>Ajothrips</i> | + | | | | | | | | |
| <i>Akheta</i> | | | | | | | | | + |
| <i>Alathrips</i> | | | | | + | | | | |
| <i>Amalothrips</i> | | | | | | | | | + |
| <i>Ameranathrips</i> | | | | | | | + | | |
| <i>Amomothrips</i> | + | | | | | | | | |
| <i>Amphithrips</i> | | | | | | | | | + |
| <i>Amphorothrips</i> | | | | | | | | | + |
| <i>Anaphothrips</i> | + | III | + | | | | | + | |
| <i>Anaphrygmothrips</i> | | | | | | | | | + |
| <i>Anarrhinothrips</i> | | | | | | | | | + |
| <i>Anascirtothrips</i> | | | | | | | | + | |
| <i>Aneristothrips</i> | | | | | | | | | + |
| <i>Aneurothrips</i> | + | | | | | | | | |
| <i>Apterothrips</i> | | | | | | | + | | |
| <i>Aptinothrips</i> | | | | | | | | + | |
| <i>Arenathrips</i> | | | | | | | | | + |
| <i>Aroidothrips</i> | | | | | | | | | + |
| <i>Arorathrips</i> | + | | | | | | | | |
| <i>Arpediothrips</i> | + | | | | | | | | |
| <i>Asphodelothrips</i> | + | | | | | | | | |
| <i>Aurantothrips</i> | + | | | | | | | | |
| <i>Ayyaria</i> | | | | | | | | + | |
| <i>Bacathrips</i> | | | | | | | | | + |
| <i>Baileyothrips</i> | | | | | | | + | | |

to be continued.

TABLE 2. (continued)

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|--------------------------|---|--------|---|---|---|---|---|---|---|
| <i>Baliothrips</i> | + | | | | | | | | |
| <i>Bathrips</i> | | VII | | | | | | | |
| <i>Belothrips</i> | + | | | | | | | | |
| <i>Bhattiana</i> | | | | | | | | + | |
| <i>Biltothrips</i> | | | | | | | | + | |
| <i>Blascothrips</i> | + | | | | | | | | |
| <i>Bolacothrips</i> | + | | | | | | | | |
| <i>Bournierothrips</i> | + | | | | | | | | |
| <i>Bradinothrips</i> | + | | | | | | | | |
| <i>Bravothrips</i> | + | | | | | | | | |
| <i>Bregmatothrips</i> | | | | | | | | + | |
| <i>Brooksithrips</i> | + | | | | | | | + | |
| <i>Capitothrips</i> | | | | | | | | | + |
| <i>Caprithrips</i> | | | | | | + | | | |
| <i>Catinathrips</i> | | | | | | | + | | |
| <i>Ceratothripoides</i> | | | | | + | | | | |
| <i>Ceratothrips</i> | | | | + | | | | | |
| <i>Cercyothrips</i> | | | | | | | | + | |
| <i>Cestrothrips</i> | | | | | | | | + | |
| <i>Chaetanaphothrips</i> | + | | | | | | | | |
| <i>Chaetisothrips</i> | + | | | | | | | | |
| <i>Charassothrips</i> | | | | | | | + | | |
| <i>Chilotherips</i> | + | | | | | | | | |
| <i>Chirothrips</i> | + | | | | | | | | |
| <i>Clypeothrips</i> | | | | | + | | | | |
| <i>Collembolothrips</i> | + | | | | | | | | |
| <i>Coremothrips</i> | | | | | | | | + | |
| <i>Corynothrips</i> | | | | | | | | | + |
| <i>Craspedothrips</i> | | | | | | | | + | |
| <i>Cricothrips</i> | | | | | + | | | | |
| <i>Ctenidothrips</i> | | | | | | | | | + |
| <i>Ctenothrips</i> | + | III-IV | | | | | | + | |
| <i>Danothrips</i> | | | | | | | | + | |
| <i>Decorothrips</i> | | | | | | | | | + |
| <i>Dendrothripoides</i> | | | | | | + | | | |
| <i>Dentothrips</i> | | | | | | | | | + |
| <i>Desertathrips</i> | | | | | | | + | | |
| <i>Deuterothrips</i> | | | | | | | | | + |
| <i>Diarthrothrips</i> | | | | | | | | + | |
| <i>Dichromothrips</i> | | | | + | | | | | |
| <i>Dictyothrips</i> | + | | | | | | | | |

to be continued.

TABLE 2. (continued)

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|-------------------------|---|--------|---|---|---|---|---|---|---|
| <i>Dikrothrips</i> | | III | | | | | | | |
| <i>Doonthrips</i> | | | | | | | | | + |
| <i>Drepanothrips</i> | | | | | | | | + | |
| <i>Dyseryngothrips</i> | + | | | | | | | | |
| <i>Echinothrips</i> | | | | | + | | | | |
| <i>Enneothrips</i> | | | | | | | + | | |
| <i>Ephedrothrips</i> | | | | | | | | + | |
| <i>Ereikethrips</i> | | III-IV | | | | | | | |
| <i>Eremiothrips</i> | + | | | | | | | + | |
| <i>Ernothrips</i> | + | | | | | | | | |
| <i>Eryngothrips</i> | + | | | | | | | | |
| <i>Euphysothrips</i> | + | | | | | | | | |
| <i>Exothrips</i> , | | | | | | | | + | |
| <i>Filipinothrips</i> | | | | | | | | + | |
| <i>Firmothrips</i> | + | | | | | | | | |
| <i>Flavidothrips</i> | | | + | | | | | | |
| <i>Florithrips</i> | + | | | | | | | | |
| <i>Foliothrips</i> | | | | | | | | + | |
| <i>Frankliniella</i> | + | | | | | | | | |
| <i>Fulmekiola</i> | + | | | | | | | | |
| <i>Furcathrips</i> | | | | | | | | | + |
| <i>Furcithrips</i> | | | | | + | | | | |
| <i>Gabanithrips</i> | | | | | | | | | + |
| <i>Glaucothrips</i> | | III | | | | | | | |
| <i>Gnomonothrips</i> | | | | | | | | | + |
| <i>Graminothrips</i> | | | | | + | | | | |
| <i>Helenothrips</i> | | | | | | | | | + |
| <i>Hemianaphothrips</i> | | | + | | | | | | |
| <i>Hengduanothrips</i> | | | | | | | | | + |
| <i>Himalthrips</i> | | | | | | | | | + |
| <i>Hyalopterothrips</i> | | | | | | | | + | |
| <i>Idolimotheis</i> | + | | | | | | | | |
| <i>Indusiothrips</i> | + | | | | | | | | |
| <i>Iridothrips</i> | + | | | | | | | | |
| <i>Isunidothrips</i> | | | | | | | | + | |
| <i>Jakthrips</i> | | | + | | | | | | |
| <i>Javathrips</i> | + | | | | | | | | |
| <i>Kakothrips</i> | + | | | | | | | | |
| <i>Karphothrips</i> | | III | | | | | | | |
| <i>Krokeothrips</i> | | | | | | | | + | |
| <i>Kurtomathrips</i> | + | | | | | | | | |

to be continued.

TABLE 2. (continued)

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---------------------------|---|---|---|---|---|----|---|---|---|
| <i>Laplothrips</i> | | | | | | | | | + |
| <i>Larothrips</i> | + | | | | | | | | |
| <i>Lefroyothrips</i> | | | | | | | | + | |
| <i>Limothrips</i> | + | | | | | | | + | |
| <i>Lomatothrips</i> | | | | | | + | | | |
| <i>Longothrips</i> | | | | | | | | | + |
| <i>Macrurothrips</i> | | | | | | | | | + |
| <i>Mecothrips</i> | + | | | | | | | | |
| <i>Megalurothrips</i> | | | | | | | | + | |
| <i>Metaxyothrips</i> | | | | | | | | | + |
| <i>Microcephalothrips</i> | + | | | | | | | | |
| <i>Monothrips</i> | | | | | | + | | | |
| <i>Moundinothrips</i> | | | | | | | | | + |
| <i>Muscithrips</i> | | | | | | | | | + |
| <i>Mycterothrips</i> | | | | | | | | + | |
| <i>Neocorynothrips</i> | | | | | + | | | | |
| <i>Neurisotheis</i> | + | | | | | | | | |
| <i>Nexothrips</i> | + | | | | | | | | |
| <i>Nigritothrips</i> | + | | | | | | | | |
| <i>Octothrips</i> | | | | | + | | | | |
| <i>Odontanaphothrips</i> | | | | | | | | + | |
| <i>Odontothripiella</i> | | | | | | | | + | |
| <i>Odontothrips</i> | | | | | | | | + | |
| <i>Oelschlaegera</i> | | | | | | | | | + |
| <i>Okajimaella</i> | | | | | + | | | | |
| <i>Organothrips</i> | | | | | + | | | | |
| <i>Oxyrhinothrips</i> | + | | | | | | | | |
| <i>Oxythrips</i> | + | | | | | | | | |
| <i>Paithrips</i> | | | | | + | | | | |
| <i>Palmiothrips</i> | + | | | | | | | | |
| <i>Parabaliorthrips</i> | + | | | | | | | + | |
| <i>Paraleucothrips</i> | | | | | | II | | | |
| <i>Parascirtothrips</i> | | | | | | | | | + |
| <i>Parascolothrips</i> | + | | | | | | | | |
| <i>Parexothrips</i> | | | | | | | | + | |
| <i>Pelikanothrips</i> | | | | | | | | | + |
| <i>Pezothrips</i> | | | | | + | | | | |
| <i>Physemothrips</i> | + | | | | | | | | |
| <i>Platythrips</i> | + | | | | | | | | |
| <i>Plesiothrips</i> | | | | + | | | | | |
| <i>Plutonothrips</i> | + | | | | | | | | |

to be continued.

TABLE 2. (continued)

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---------------------------|---|--------|---|---|---|---|---|---|---|
| <i>Priesneriola</i> | | | | | | | | | + |
| <i>Prionothrips</i> | + | | | | | | | | |
| <i>Projectothrips</i> | + | | | | | | | | |
| <i>Proscirtothrips</i> | | | | | | | | + | |
| <i>Prosoponaphothrips</i> | + | | | | | | | | |
| <i>Prosopothrips</i> | + | | | | | | | | |
| <i>Psectrothrips</i> | + | | | | | | | | |
| <i>Pseudanaphothrips</i> | + | | | | | | | | |
| <i>Pseudothrips</i> | | | | | | | + | | |
| <i>Pseudoxythrips</i> | | | | | | | | + | |
| <i>Psilothrips</i> | | III-IV | | | | | | | |
| <i>Psydrothrips</i> | | | | | | | + | | |
| <i>Pteridothrips</i> | | | | + | | | | | |
| <i>Ranjana</i> | | | | | | | | | + |
| <i>Rhabdorthrips</i> | | | | | | | | | + |
| <i>Rhamphiskothrips</i> | | | | | | | | | + |
| <i>Rhamphothrips</i> | | | | | | | | + | |
| <i>Rhaphidothrips</i> | + | | | | | | | | |
| <i>Rhinothripiella</i> | | | | | | | | | + |
| <i>Rhinothrips</i> | | | | | | + | | | |
| <i>Rubiothrips</i> | + | | | | | | | | |
| <i>Salpingothrips</i> | + | | | | | | | | |
| <i>Sciothrips</i> | + | | | | | | | | |
| <i>Scirtidothrips</i> | | | | | | | | + | |
| <i>Scirtothrips</i> | | | | | | | | + | |
| <i>Scolothrips</i> | + | | | | | | | | |
| <i>Sericopsothrips</i> | | | | | | | | | + |
| <i>Siamothrips</i> | | | | | | | | + | |
| <i>Simulothrips</i> | | | | | + | | | | |
| <i>Sitothrips</i> | + | | | | | | | | |
| <i>Smeringothrips</i> | | | | | | | | | + |
| <i>Smilothrips</i> | | | | | | | | | + |
| <i>Sminyothrips</i> | + | | | | | | | | |
| <i>Solanithrips</i> | + | | | | | | | | |
| <i>Sorghothrips</i> | | | | | | | | + | |
| <i>Sphaeropothrips</i> | + | | | | | | | | |
| <i>Stannardia</i> | | | | | | | | | + |
| <i>Stenchaetothrips</i> | + | | | | | | | | |
| <i>Stenothrips</i> | + | | | | | | | | |
| <i>Synaptothrips</i> | | | | | | | | + | |
| <i>Systemothrips</i> | + | | | | | | | | |

to be continued.

TABLE 2. (continued)

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|-------------------------|----|--------|---|---|----|---|----|----|----|
| <i>Taeniothrips</i> | + | | | | | | | | |
| <i>Takethrips</i> | | | | | | | | | + |
| <i>Tamaricothrips</i> | + | | | | | | | | |
| <i>Tameothrips</i> | | | | | | | | | + |
| <i>Tenothrips</i> | + | | | | | | | | |
| <i>Theilopodothrips</i> | | | | | | | | + | |
| <i>Thermothripoides</i> | | | | | | | | | + |
| <i>Thermothrips</i> | + | | | | | | | | |
| <i>Thrips</i> | + | | | | | | | | |
| <i>Tmetothrips</i> | + | | | | | | | | |
| <i>Toxonothrips</i> | | III-IV | | | | | | | |
| <i>Trachynotothrips</i> | | | | | + | | | | |
| <i>Trichromothrips</i> | | | | | + | | | | |
| <i>Tusothrips</i> | | | | | | + | | | |
| <i>Vulгатоthrips</i> | | | | | | | | | + |
| <i>Watanabeothrips</i> | | | | | + | | | | |
| <i>Wegenerithrips</i> | | | | | | | | | + |
| <i>Xerothrips</i> | | | | | | | + | | |
| <i>Yoshinothrips</i> | | | | | + | | | | |
| <i>Zurstrassenia</i> | | | | + | | | | | |
| Totals | 80 | 9 | 4 | 5 | 18 | 7 | 10 | 44 | 39 |

also have multiple pore plates in males, including *Echinothrips*, *Ceratothripoides*, and *Pezothrips* (Fig. 24), as well as *Organothrips indicus* (Fig. 29) and the closely related genus *Graminothrips*. In contrast, *Organothrips wrighti* has a large oval pore plate on sternites III–VII (Fig. 30).

In Thripinae, the most common condition of the male pore plates is transversely oval on sternites III–VII, although their size and the number of sternites involved varies between species. For example among the ten species of *Ctenothrips* these structures are reported as absent in some species, but present on III–VII in some and on III–IV in others. Moreover, in several other genera pore plates are present on only one or two sternites (Table 2 Column 4). However, males of most species in the *Thrips* genus-group (*Baliothrips*, *Bolacothrips*, *Bournierothrips*, *Ctenidothrips*, *Ernothrips*, *Fulmekiola*, *Larothrips*, *Microcephalothrips*, *Rhinothripiella*, *Sphaeropothrips*, *Stenchaetothrips*, *Stenothrips*, *Thrips* and *Toxonothrips*) have pore plates on sternites III–VII (Figs 35–38), although these are only on III–V in *Thrips tabaci*, III–IV in *Toxonothrips*, and in *Larothrips* the pore plates are sometimes reduced or even absent (Bournier, 1994); males remain unknown in *Ctenidothrips* and *Rhinothripiella*. Similarly, males in the *Frankliniella* genus-group (*Firmothrips*, *Frankliniella*, *Iridothrips*, *Kakothrips*, *Parabaliothrips*, *Pelikanothrips*, *Pseudanaphothrips* and *Sitothrips*) usually have transversely oval pore plates on sternites III–VII (Figs 17, 18, 22, 23), apart from one species of *Parabaliothrips* which has none; the male is not known for *Pelikanothrips*. The interesting variation in form of the pore plates in *Anaphothrips* males was illustrated by Mound & Masumoto (2009). Of the 40 species in this genus known from Australia, 20 have distinctive U-shaped pore plates that vary greatly in size between species, sometimes even extending around the margins of the sternites. However, in a few species the pore plates are weakly curved or almost straight, in one species the pore plates are replaced by a pair of small circular areas close to the anterior margin on a single sternite, and in six species they are completely absent.

Males in a few genera, such as *Dichromothrips* (Fig. 28), have only two or three pore plates on one or more sternites (Table 2 Column 6). However, relationships between these genera are not clear, and the homologies involved (whether derived by subdivision from a single pore plate, or by reduction from or fusion of multiple pore plates) are not clear. Similarly, it is not known if each of the small multiple pore plates in species such as *Pezothrips kellyanus* are subtended by one or more glandular cells (Webster et al., 2006). Equally unclear are the homologies and relationships of those genera in which pore plates are present on, or anterior to, the antecostal ridge (Fig. 20) of one or more sternites (Table 2 Column 8). The pore plates of *Tusothrips sumatrensis* are greatly reduced (Fig. 31) on the anterior margin of the antecostal ridge.

Males in one group of New World genera are particularly unusual (*Ameranathrips*, *Apterothrips*, *Baileyothrips*, *Catinathrips*, *Charassothrips*, *Desertathrips*, *Enneothrips*, *Pseudothrips*, *Psydrothrips* and *Xerothrips*), in that although they lack pore plates, they have a specialized opening on or close to the antecostal ridge of sternite III that is associated with an internal gland (Fig. 9). There have been no investigations into the structure of these organs, but it seems probably that they are independently derived from sternal pore plates.

Thripinae females with sternal pore plates

Although sternal pore plates are primarily associated with Thysanoptera males, this sex-linkage is occasionally inverted, with male-like pore plates occurring on sternite III (more rarely III and IV) in females of several unrelated genera. Unfortunately, it is not known if the internal structure of pore plates is similar in males and females, thus it is not possible to be sure of their homology. Females of at least five species in the genus *Oxythrips* have a pore plate, and this is true also of the single species in the closely related genus *Macrurothrips* (zur Strassen, 2003), as well as those in the related genus *Chilothrips* (Hoddle et al., 2008). However, this is the only good example of the presence of these structures in females of species that are related phylogenetically. Females of *Chaetanaphothrips signipennis*, a widespread pest of bananas, consistently have a transverse pore plate (Fig. 27) on the third sternite, but this is not found in any of the other 19 species in the genus. *Cyrlthrips*, a related monotypic genus, also has a similar structure in females (Tree & Mound, 2009), but in the large and worldwide genus *Thrips* only one species, *Thrips knoxi*, is known to have females with a pore plate on sternite III (Fig. 39). Even in this species, the pore plate is present or absent in different populations (Mound & Masumoto, 2005). Similar inconsistency in this character state occurs in females of *Frankliniella australis*, one of very few species in this large genus that have females usually with a pair of pore plates on the third sternite (Fig. 26). Females of *Limothrips cerealium*, the most abundant thrips on grasses in Western Europe, typically have no pore plates, but in some populations in the Mediterranean region females have a pore plate on sternites III and IV (Mound & Palmer, 1974).

Pore plates in females have not been demonstrated to have any functional significance, and they possibly represent some form of genetic aberration. Such inversion of a sex-linked character state has been reported occasionally amongst other Thysanoptera. For example, in the genus *Machatothrips* (Phlaeothripidae) with 14 described species from the Old World tropics, females but not males bear a row of tubercles on the inner margin of the fore femora. However, in two species of this genus from Malaysia males sometimes have similar although rather weak tubercles (Palmer & Mound, 1978).

Discussion

The objective of this study was to provide a factual background for future studies on the presence and functional significance of chemical communication among various Thysanoptera species, and to provide the possibility of such studies being placed within a phylogenetic context. The body structure and geographic distribution of members of the *Thrips* genus-group and *Frankliniella* genus-group suggest that these represent two of the most recently derived groups of Thripinae (Mound, 2002). In both of these highly derived taxa male sternal pore plates are present consistently, but this in no way should be taken as implying that the

presence of pore plates is itself a highly derived character state. Similar structures occur in many unrelated species in three of the four subfamilies of Thripidae, and are actually absent in scarcely 30 percent of Thripinae genera, the largest subfamily (Table 2). This suggests that within the family Thripidae, absence of pore plates is probably a derived condition. However, as with other “loss-apomorphies”, such as the loss of long setae on the pronotum (Mound & Masumoto, 2009), absence of pore plates is likely to have arisen several times among the members of this family. This loss of pore plates in males is presumably associated in some way with differences in sexual behaviour.

Presence and absence of pore plates between pairs of closely related species, such as *Limothrips cerealium* and *Limothrips denticornis*, might provide a basis for behavioural comparisons. Considering this particular pair of species, *L. denticornis* lacks male pore plates and is reported to indulge in pupal rape, with males apparently copulating with female pupae (Bournier, 1956). Unfortunately, extensive studies (Lewis, 1959) on the life cycle of the more abundant grass thrips, *L. cerealium*, in which males have sternal pore plates, did not investigate sexual behaviour, although anecdotal evidence suggests that aggregations occur in this species.

The lack of detailed behavioural studies on so many Thysanoptera limits any conclusions that might be drawn from morphological comparisons. For example, some species in the Thripidae genera *Mycterothrips* and *Filipinothrips* exhibit extreme sexual dimorphism in their antennae, those of males bearing numerous and prominent sensoria and setae (Masumoto & Okajima, 2006; Tyagi et al., 2008). However, males in neither of these genera have sternal pore plates. Masami Masumoto (in litt. 2009) has informed me that in mountainous areas of Japan *Mycterothrips consociatus* males form aggregations. The possible function in such species of their bizarre antennae, how they are deployed in sexual behaviour and the source of pheromones that they are presumably adapted to detect, remains conjectural. Similarly unrecorded is the structural diversity of male genitalia in Thripidae. It may be significant that certain genera in which the genitalia bear species-specific structures (e.g. *Odontothrips* and *Rhamphothrips*) lack sternal pore plates in males. Thus, despite over 100 years of descriptive taxonomy on Thysanoptera, there is a continuing lack of observations on so many aspects of their biology (Mound, 2004).

Acknowledgements

The observations recorded here were based primarily on slide-mounted specimens in the collections at the Natural History Museum, London, the Forschungsinstitut Senckenberg, Frankfurt, and the US National Museum of Natural History, Washington, and I am grateful to the curators of those collections for their many courtesies: Jon Martin, Richard zur Strassen and David Nickle. I am particularly grateful to William Kirk for encouraging me to assemble the data, also to Bruce Heming, Masami Masumoto and William Kirk for informative comments on earlier drafts. The photomicrographs were taken using a Leica DM2500 Differential Interference Contrast microscope, and the digital images were processed with Automontage software.

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